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GEOGRAPHIC VARIATION IN THE RIBBED FROG, *ASCAPHUS TRUEI*

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In the Pacific Northwest, from British Columbia and Montana to northern California, occurs the most remarkable of North American frogs. *Ascaphus truei* Stejneger is not only the most primitive New World frog, but it also possesses a tadpole unique among Nearctic Salientia. Heretofore, but a single named population has been recognized within the genus *Ascaphus*. While it is the primary purpose of this paper to demonstrate the existence of three recognizable populations of *Ascaphus*, a brief historical and systematic introduction appears to be useful.

The Ascaphidae, as recognized by Noble (1931: 485, where called Liopelmidae), include but two genera, *Leiopelma* and *Ascaphus*. The first-known genus, *Leiopelma*[1], is restricted to New Zealand, from whence three forms have been described: *L. hochstetteri* Fitzinger, *L. hamiltoni* McCulloch, and *L. archeyi* Turbott. The primitive nature of *Leiopelma* was not at first understood, principally because of the then-rudimentary state of frog classification. Fitzinger (1861) compares the genus with *Telmatobius* and *Cyclorhamphus*, two neotropical genera now referred to the Leptodactylidae. Steindachner (1867: 33) places *Leiopelma* in the "Bombinatoridae," a heterogeneous group assembled by Günther, and based chiefly on dentition, hympanum, and toe-webbing. Boulenger (1882: 447) appears to have been the first to recognize that *Leiopelma* belongs with the primitive, ribbed frogs, but his later denial of the presence of rudimentary ribs, and consequent placement of *Leiopelma* in the "Cystignathidae" (= Leptodactylidae), in 1910 (p. 150, footnote), has never been properly explained. The work of Noble (1922) reinstated *Leiopelma* among the ribbed frogs, but he separated this genus and *Ascaphus* from the more advanced Discoglossidae, in which all the ribbed frogs had previously been placed (Noble, 1931: 485).

On the other hand, *Ascaphus*, unlike *Leiopelma*, was recognized as a primitive frog from the very first. The unique type specimen was obtained by Cloudsley Rutter of Stanford University, during the course of some ichthyological work he was doing for the U. S. Fish Commission

[1]This generic name is spelled *Liopelma* by most recent writers, following Boulenger (1882: 447). Myers and Carvalho (1945: 17, footnote 5) called attention to this error, although they did not have Fitzinger's original paper in hand. While the classically correct transliteration of the name would be *Liopelma*, Fitzinger (1861: 218) spelled it *Leiopelma*, and the International Rules require the retention of this orthography.

in western Washington State. The type was forwarded to Washington, probably to the headquarters of the Fish Commission, whence it was turned over to the National Museum. The specimen was described by Stejneger in 1899, as *Ascaphus truei,* and referred to the Discoglossidae. This discovery, the most important in Nearctic batrachology, led Stejneger to write his paper on the geographical distribution of the Discoglossids (1905).

For a number of years *Ascaphus* remained a very rare frog. However, as its habitat became known, more specimens became available, so that over the course of the fifty years since its original description *Ascaphus* has become a relatively well-known frog. As early as 1912, Van Denburgh published a detailed note on the skeletal antomy, while Mrs. Gaige wrote at considerable length (1920) on the life-history and ecology, on the basis of her observations in the Olympic Peninsula. Noble (1922, 1931) published some notes on the life-history and breeding of the species from live material and information supplied by Phillips G. Putnam. The cranial anatomy has been investigated by de Villiers (1934), and a number of notes have been published by Storer (1925), Slevin (1928), Myers (1931, 1943), Smith (1932), the Wrights (1933, 1942), and at least 23 other writers.

Yet, despite these many contributions to a rapidly-growing literature, the morphological variations of *Ascaphus*—especially the extent and nature of these variations with respect to geographic distribution—remain scarcely known. In part, this doubtless arises from the fact that there are comparatively few adult (post-metamorphic) specimens in collections, and probably also because the habits of this animal are such that its range is still imperfectly known, with many gaps yet to be filled. Myers has suspected since 1931 that the California population of *Ascaphus* differs racially from that of Oregon and Washington, but before Mittleman knew of this he already had the present study well under way. He then invited his western colleague to assume joint authorship. All mensural and statistical treatments have been done by Mittleman, but the conclusions expressed herein, as well as the new names proposed, have been authored jointly.

A study of 65 post-metamorphic and 166 larval specimens of *Ascaphus,* from all parts of the range of this species, indicates that it is composed of three vicarious races: the typical form, occurring in western Oregon and Washington; another race occupying the Northern Rocky Mountain Province in Idaho, Montana, and adjacent British Columbia; a third race restricted to a few counties in northern California. The differences among these three races are quantitative and/or meristic, and although in some cases they are slight in terms of absolute quantities, they are nonetheless of such a constant nature as to permit the positive separation of 88% of the post-metamorphic specimens studied. No qualitative differences have been found among the populations studied, nor do color or pattern provide useful dichotomous characters.

The distinguishing unitary traits of the three races are the number of vomerine teeth, and the relative dimensions of the eye and head width. No ontogenetic or sexual variations have been found in these characters, so that all tabulations and comparisons are made on the basis of post-metamorphic specimens of all ages and of both sexes.

Vomerine Teeth

The vomerine teeth in *Ascaphus truei* vary from 1 to 17 per series. There is, as in most amphibians, a considerable variation in the number of teeth per series in individuals, e.g., there is often a considerable discrepancy in the number of teeth on one side, as compared to the other. Thus, in order to facilitate comparisons between individuals and populations, the tooth counts of both sides have been combined to yield a single count reflecting the total number of vomerine teeth in the specimen. The full range of variation in the combined vomerine counts of 52 post-metamorphic *Ascaphus* from all parts of the range of this species is as follows:

2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	N
f 4		4	2	3	3	3	2	3		7	3	3	2	2	2		51		1	1								1	52

Combined Vomerines

Examination of 13 adult specimens of *Ascaphus truei* from western Washington and Oregon shows that the combined vomerine counts vary from 8 to 30. Nine specimens from various southern British Columbia localities have a range of 8 to 21 teeth, while in 13 specimens from Idaho and Montana the spread is from 9 to 22. No significant statistical differences exist between any of these populations so far as the vomerine count is concerned. However, in 17 adult specimens from northern California, the combined vomerine count is much lower, as is also the range of variation, the observed spread being 2 to 8 teeth per specimen. The combined vomerine count is 7 or less in 16 out of 17 Californian specimens, but is 8 or more in all 35 specimens from Oregon, Washington, British Columbia, Idaho, and Montana. Hence, 51 specimens out of 52 (= 98%) can be identified as to a Californian or non-Californian provenance on the basis of the vomerine count alone. A chi-square value of 47.5 attests to the highly significant association between the combined vomerine count and geographic origin in these samples.

Relative Size of the Eye

The diameter of the eye has been taken as the horizontal distance between the anterior and posterior junctures of the lids. Measurements were made with a vernier caliper under low-power (17×) binocular magnification. The ratio of the horizontal diameter of the eye to the snout-vent length (hereafter referred to as the eye/SV ratio) shows a small absolute variation, being in 60 specimens of *Ascaphus* from all parts of the range, as follows:

f	eye/SV ratio (%)
3	10.00 - 10.99
14	11.00 - 11.99
13	12.00 - 12.99
12	13.00 - 13.99
13	14.00 - 14.99
5	15.00 - 15.99
N = 60	

As in the case of the vomerine counts, the eye/SV ratios show certain geographic variations. Thus, the 13 Oregon-Washington specimens vary from 11.2 to 13.0%; the British Columbia series shows a variation of 10.44 to 13.60%, while 14 specimens from Idaho and Montana show a range of 10.7 to 13.4%. The California population is again distinctive by virtue of having a proportionately larger eye, since the eye /SV ratio in 24 specimens varies from 12.5 to 15.9%. In 23 out of the 24 Californian specimens the eye/SV ratio is 13.6% or more, while in 35 specimens out of 36 from other areas this critical ratio is 13.5% or less. Thus, 58 out of 60 specimens (= 96%) can be identified as to a Californian or non Californian origin on the basis of the eye/SV ratio.

However, the non Californian specimens are not themselves homogeneous with respect to their eye/SV ratios. Although there is no perceptible difference between specimens from Oregon and Washington in the relative size of the eye, there is a discernable and significant trend toward a higher eye/SV ratio in specimens from Idaho, Montana, and British Columbia. Oregon and Washington specimens have ratios varying from 11.2 to 13.0%, with 10 out of 13 specimens from these states having ratios of 11.85% or less. In specimens from Idaho, Montana, and British Columbia the eye/SV ratio ranges from 10.44 to 13.60%, with 16 specimens out of 23 having a ratio higher than 11.85% (12.31% or more). A total of 26 specimens out of 36 (= 72%) in these two samples can be correctly separated as to their geographic provenance on the basis of the eye/SV ratio. The observed differences in the eye/SV ratios of these two populations are statistically significant (chi-square = 7.19).

Relative Head Width

The width of the head has been measured at the point of greatest breadth, immediately behind the eyes. Measurements were taken with a vernier caliper under 17X binocular magnification. The ratio of the head width to the snout-vent length (hereafter referred to as the HW/SV ratio) shows a moderate absolute variation, ranging from 32.5 to 42.6%, as follows:

f	HW/SV ratio (%)
2	32.00 - 32.99
5	33.00 - 33.99
7	34.00 - 34.99
5	35.00 - 35.99
6	36.00 - 36.99
3	37.00 - 37.99
7	38.00 - 38.99
8	39.00 - 39.99
8	40.00 - 40.99
5	41.00 - 41.99
4	42.00 - 42.99
N = 60	

Each of the various samples discussed heretofore has a characteristic range of variation in its HW/SV ratio. Thus, Oregon-Washington specimens show a range of 32.5 to 39.4%, while British Columbia speci-

mens vary from 33.4 to 37.7%, and the Idaho-Montana samples show a spread of 34.2 to 39.4%. California specimens are again distinctive by virtue of having a relatively wider head, the range of the HW/SV ratio being 38.4 to 42.6%.

Despite apparently broad overlaps in the HW/SV ratios of the various samples, there are actually very significant differences in the relative head widths of the populations involved. Hence, 23 out of 24 California specimens have HW/SV ratios of 39.0% or more, while in 34 out of 36 non-Californian specimens the HW/SV ratio is 38.7% or less. These critical ratios will separate 57 specimens out of 60 (= 95%), as to a Californian or non-Californian origin. A chi-square value of 47.4 attests to the highly significant association between geographic provenance and proportionate head width.

In a similar vein, it is found that 11 out of 13 Oregon-Washington specimens have an HW/SV ratio of 35.2% or less, while 18 out of 23 specimens from Idaho, Montana, and British Columbia have ratios of 35.6% or more. Again, with 29 specimens out of 36 (= 80.5%) being geographically identifiable on the basis of their HW/SV ratios, the significant association between this ratio and geographic origin is reaffirmed (chi-square = 13.3).

Larvae

Despite the differences existing among the several populations of *Ascaphus truei*, as discussed heretofore, the larvae are remarkably stable in size, proportions, color, pattern, and tooth-row counts. In fact, it has not been possible to determine any dichotomous differences in tadpoles from widely separated parts of the range of the species (*sensu lato*).

Authors who have had occasion to discuss the larvae of *Ascaphus truei* have described the tooth rows as being 3/10, except Smith (1932: 100), who reports a specimen from St. Regis Pass, Montana as having the tooth rows 3/9. Careful study of 123 larvae from all parts of the range of *Ascaphus* shows that the tooth count is either 3/11 or 3/12. The last lower rows, where they encroach on the lower (posterior) lip are exceedingly minute, and occasionally are imperfect. Nonetheless, careful examination under relatively low magnification (25.5X) will reveal these teeth.

Counts of 11 or 12 lower tooth rows occur with approximately equal frequency throughout the range of *Ascaphus*, as will be seen in the following tabulation:

Lower Tooth Rows

Locality	11	12	Total
California	12	9	21
Washington	6	0	6
Idaho	1	0	1
Montana	33	39	72
British Columbia	10	13	23
	62	61	123

There is no perceptible correlation or association between tooth-row counts and size in *Ascaphus* larvae. The full range of size variation (overall length, snout to tip of tail) observed in larvae is from 15 mm.

(Park Creek, Glacier National Park, Mont.), to 60 mm. (Ole Creek, Glacier National Park).

From our studies of the several populations discussed here, we conclude that *Ascaphus truei* is a polytypic species composed of three annectant, vicarious races. The population inhabiting the northern parts of the Cascade-Sierra Province and the Pacific Border Province in Oregon and Washington is indistinguishable from Stejneger's type of *truei* (USNM 25979, Humptulips, Grays Harbor Co., Wash.), whereas the population occurring in the southern parts of these Provinces (in Del Norte, Siskiyou and Humboldt counties, Calif.) is markedly different, as is also the form which ranges through the Northern Rocky Mountains Province in Idaho, Montana (probably also extreme eastern Oregon and Washington), and adjacent British Columbia. Accordingly, we restrict the name *truei* to the western Oregon-Washington population, and propose that the other two forms be recognized as subspecies. Our definition of *truei*, and descriptions of the two new races follow.

Ascaphus truei truei Stejneger

1899 *Ascaphus truei* Stejneger, Proc. U. S. Nat. Mus., 21: 900, pl. 39. Type locality: Humptulips, Grays Harbor (formerly Chehalis) County, Wash.; Dickerson, 1906, Frog Book, p. 51; Van Denburgh, 1912, Proc. Calif. Acad. Sci., 4 (3): 259; Camp, 1917, Copeia: 13; Stejneger and Barbour, 1917, Check-list N. Amer. Amph. Rept., p. 25; *ibid.*, ed. 2, 1923, p. 22; *ibid.*, ed. 3, 1933, p. 25 (*part.*); *ibid.*, ed. 4, 1939, p. 28 (*part.*); *ibid.*, ed. 5, 1943, p. 36 (*part.*); Gaige, 1920, Occ. Pap. Mus. Zool. Univ. Mich., 84: 1; Van Winkle, 1922, Copeia: 4; Noble, 1922, Copeia: 4; Storer, 1925, Univ. Calif. Publ. Zool., 27: 143 (*part.*); Slevin, 1928, Occ. Pap. Calif. Acad. Sci., 16: 79 (*part.*); Slater, 1931, Copeia: 62; Noble and Putnam, 1931, Copeia: 97; Svihla and Svihla, 1932, Copeia: 38; Svihla and Svihla, 1933, Copeia: 37; A. Svihla, 1933, Copeia: 39; Wright and Wright, 1933, Handbook of Frogs and Toads, p. 36 (*part.*); *ibid.*, ed. 2, 1942, p. 44 (*part.*); Slater, 1934, Copeia: 140; Graf, Jewett, and Gordon, 1939, Copeia: 102.

Diagnosis: Combined vomerines 8-30; eye/SV ratio 11.2-13.0% (11.85% or less in 77% of specimens); HW/SV ratio 32.5-39.4% (35.2% or less in 85% of specimens).

Range: Oregon and Washington, in the Cascade-Sierra and Pacific Border Provinces.

Specimens studied: 48, as follows:

OREGON

Curry County: N. side of Rogue River, 11. mi. above mouth (MVZ[2] 17162).

Klamath County: Castle Creek, Crater Lake Nat. Pk. (SU 3920); Copeland Creek, Crater Lake Nat. Pk. (USNM 95230-1); Bybee Creek, Crater Lake Nat. Pk. (USNM 95226-9).

[2]Abbreviations for collections: MVZ = Museum of Vertebrate Zoology: SU = Natural History Museum, Stanford University; USM = United States National Museum; CNHM = Chicago Natural History Museum; CAS = California Academy of Sciences; PMBC = Provincial Museum of British Columbia; ROMZ = Royal Ontario Museum of Zoology.

WASHINGTON

Chelan County: Icicle Creek (USNM 103708; 3 spec.).
Clallam County:Olympic Hot Springs (CNHM 27117-8).
Grays Harbor County: Humptulips (USNM 25979, TYPE).
Jefferson County: Mt. Steel (USNM 63387); Dosewallips River (USNM 64345).
Lewis County: Tilton River (CNHM 27119; 2 spec.).
Mason County: Staircase Camp (MVZ 8497-8); McTaggart Creek (USNM 67121-3; 63388-90); Laundry Creek (USNM 67120).
Pierce County: Mt. Rainier (USNM 62434, 62436, 62438, 62450); Tacoma Creek (USNM 104423-4); Stevens Creek (USNM 104425); Nickel Creek (USNM 104426).
Snohomish County: No locality (CNHM 41298; 2 spec.).
Yakima County: Outlet of Dewy Lake, S. of Naches Pass (SU 9285-7).
No specific locality: "Western Washington" (SU 3091-5, 3761; 3 spec.).

Ascaphus truei californicus, n. ssp.

1917 *Ascaphus truei* Grinnell and Camp, Univ. Calif. Publ. Zool., 17: 140; Stejneger and Barbour, 1923, Check-list N. Amer. Amph. Rept., p. 22 (*part.*); *ibid.*, ed. 3, 1933, p. 25 (*part.*); *ibid.*, ed. 4, 1939, p. 28 (*part.*); *ibid.*, ed. 5, 1943, p. 36 (*part.*); Storer, 1925, Univ. Calif. Publ. Zool., 27: 143 (*part.*); Slevin, 1928, Occ. Pap. Calif. Acad. Sci., 16: 79 (*part.*); Myers, 1931, Copeia: 56; Wright and Wright, 1933, Handbook Frogs and Toads, p. 36 (*part.*); *ibid.*, ed. 2, 1942, p. 44 (*part.*); Shapovalov, 1937, Copeia: 234; Wood, 1939, Copeia: 110; Myers, 1943, Copeia: 126.

Diagnosis: Combined vomerines 2-8 (7 or less in 94% of specimens); eye/SV ratio 12.5-15.9% (13.6% or more in 96% of specimens); HW/SV ratio 38.4 to 42.6% (39.0% or more in 96% of specimens).
Range: Del Norte, Humboldt, and Siskiyou counties, California.
Holotype: MVZ 19142 ♀, near Klamath, Del Norte County, Calif; collected by W. F. Wood, November 4, 1933.
Paratypes: See list of specimens studied.
Specimens studied: 50, as follows:

CALIFORNIA

Del Norte County: Klamath (CNHM 31909); Wilson Creek, near Klamath (CNHM 31912); tributary of Wilson Creek, 8.5 mi. N. of Klamath (MVZ 29790-3, 29795, 29797-8, 29801-3); 8 mi. NE of Crescent City (CAS 80135).
Humboldt County: Ascaphus Creek, 0.5 mi. N. of road to Holmes, on Redwood H'way (SU 7371-2, 7390-9); Prairie Creek, 11 mi. N. of Orick (CNHM 31910-11); 8.6 mi. N. of Weott (SU 4636-42); near Scotia (USNM 93779; 4 spec.); 10 mi. N. of Orick (CAS 80159-62); 10 mi. W. of Orick (CAS 78812-3).
Siskiyou County: French Creek (SU 2190); "Siskiyou Mts." (USNM 45362); Mill Creek Park (CAS 81297-300).

Remarks: While it may seem strange that a political boundary, the California-Oregon line, should separate two races (*truei* and *californicus*), it should be pointed out that this particular political boundary is, to some extent, a biogeographical one as well. The Siskiyou Moun-

tains and associated ranges, which rise along the state line, form a barrier which can be seen in the distribution of a number of animal populations. These mountains delimit the northern range of *Batrachoseps* and of *Aneides flavipunctatus* (see Myers and Maslin, 1948, Proc. Biol. Wash., 61: 127), and come very close to marking the division between the subspecies of *Bufo boreas* and *Rana aurora*. It may be noted that these mountains limit the southward extension of *Rana pretiosa* (west of the Cascade-Sierra range), and the northward extension of *Scaphiopus* in the Sacramento Valley. In addition, this natural barrier seems to mark a subspecies boundary in *Triturus granulosus*, and *T. rivularis* is not known to pentrate it from the south.

Ascaphus truei montanus, n. ssp.

1932 *Ascaphus truei* Smith, Copeia: 100; Stejneger and Barbour, 1933, Check-list N. Amer. Amph. Rept., p. 25 (*part.*); *ibid.*, ed. 4, 1939, p. 23 (*part.*); *ibid.*, ed. 5, 1943, p. 36 (*part.*); Wright and Wright, 1933, Handbook Frogs and Toads, p. 36 (*part.*); *ibid.*, ed. 2, 1942, p. 44 (*part.*); Linsdale, 1933, Copeia: 223; Donaldson, 1934, Copeia: 184; Ricker and Logier, 1935, Copeia: 46; Slater, 1941, Occ. Pap. Coll. Puget Sound, 14: 85; Rogers and Jellison, 1942, Copeia: 10; Slipp and Carl, 1943, Copeia: 127; Carl and Cowan, 1945, Copeia: 52.

Diagnosis: Combined vomerines 8-22; eye/SV ratio 10.44-13.60% (12.31-13.60% in 70% of specimens); HW/SV ratio 33.4-39.4% (35.6 — 38.6% in 74% of specimens).

Range: The Northern Rocky Mountains Province in Idaho, western Montana, probably extreme eastern Oregon and Washington, and adjacent British Columbia.

Holotype: USNM 102505 ♂, tributary of Lincoln Creek, Glacier National Park, Flathead County, Montana; collected by Leonard P. Schultz.

Paratypes: See list of specimens studied.

Specimens studied: 122, as follows:

IDAHO

Adams County: 0.5 mi. E. of Black Lake, 6000 ft. (MVZ 12340-3; 12345).

Benewah County: East Fork of Charley Creek, near Emida (CNHM 43583).

Washington County: 1.0 mi. NE of Heath, on SW slope of Cuddy Mt., 4000 ft. (MVZ 12344, 12336).

MONTANA

Flathead County: Midvale Creek, near Glacier Nat. Pk. (Univ. Wash., 2 spec.); Tributary to Lincoln Creek, Glacier Nat. Pk. (USNM 102506-7); Hidden Lake, Glacier Nat. Pk. (USNM 102503); Lake Evangeline, Glacier Nat. Pk. (USNM 102508-9); Coal Creek, Glacier Nat. Pk. (USNM 102510-11; 30 spec.); Ole Creek, Glacier Nat. Pk. (USNM 102512; 12 spec.); Park Creek, Glacier Nat. Pk. (USNM 102514; 55 spec.); Dutch Creek Nat. Pk. (USNM 102513; 16 spec.); Muir Creek, Glacier Nat. Pk. (USNM 102504).

BRITISH COLUMBIA

Cascade Creek, 5 mi. NW of Hatzic (PMBC 634, 692); Cultus

Lake, Fraser River Valley District (ROMZ 5382-5; 5391-6; 5389-90; 5497, 4 spec.; 5399-5409; 3459; 7194-8).
Also, three additional specimens from southern British Columbia, to be reported by Dr. G. Clifford Carl.

The following key to the races of *Ascaphus truei* will correctly identify 85% of the post-metamorphic specimens seen:

Key to the Races of *Ascaphus truei*

1. Eye/SV ratio 13.6% or more; combined vomerine count 7 or less. Del Norte, Humboldt, and Siskiyou counties, California. ..... *Ascaphus truei californicus*, n. ssp.
   Eye/SV ratio 13.5% or less; combined vomerine count 8 or more. Provenance non-Californian 2
2. Eye/SV ratio 11.85% or less; HW/SV ratio 35.2% or less. Oregon and Washington, in the Cascade-Sierra and Pacific Border Provinces. ..... *Ascaphus truei truei* Stejneger
   Eye/SV ratio 12.31-13.50%; HW/SV ratio 35.6-38.6%. Northern Rocky Mountains Province in Idaho, western Montana, adjacent British Columbia, and probably extreme Washington and Oregon. ..... *Ascaphus truei montanus*, n. ssp.

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